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students and teachers; for example, such as the following:

"The Remainder Term in a Certain Development of  $F(a+x)$ ," by Professor R. D. Carmichael, Indiana University.

"A Geometric Interpretation of the Function  $F$  in Hyperbolic Orbits," by Professor W. O. Beal, Illinois College.

"Certain Theorems in the Theory of Quadratic Residues," by Professor D. N. Lehmer, University of California.

"Some Inverse Problems in the Calculus of Variations," by Dr. E. J. Miles, Yale University.

"Amicable Number Triples," by Professor L. E. Dickson, University of Chicago.

H. E. SLAUGHT,  
Managing Editor

#### BRANCH MOVEMENTS INDUCED BY CHANGES OF TEMPERATURE<sup>1</sup>

THAT changes occur in the linear dimensions of metals following fluctuations in the temperature is common knowledge, but that similar changes result in wood and living trees is not so generally known. Pure water has its smallest volume at 4° C., and lowering the temperature further increases its volume until it freezes; while ice contracts regularly with decreasing temperature and at a greater rate than any of the metals. It is generally supposed that marked changes in temperature have some effect upon the volume of tree trunks because radical clefts occur so frequently in severe winters and old clefts close during the middle of warm winter days and open again as the temperature sinks during the night. Since freezing water often bursts its container it is popularly held that such tree trunks are burst by the expansion of the freezing water in them. Caspary<sup>2</sup> has shown this

<sup>1</sup> This review of the literature of branch movements and observations grew out of a study of crown-rot of fruit trees and is published separately because it is only indirectly related to the main theme.

<sup>2</sup> R. Caspary, "Ueber Frostspalten," *Bot. Zeit.*, 13: 449-62, 473-82, 489-500, 1855; "Neue Untersuchungen über Frostspalten," *Bot. Zeit.*, 15: 329-35, 345-50, 361-71, 1857.

to be erroneous by calling attention to the facts that ice contracts as the temperature sinks while clefts in tree trunks open farther and farther as the temperature drops, *i. e.*, were the opening of the clefts due to the formation of ice they would close again as the temperature sank lower. As a matter of fact tree trunks begin contracting above the freezing point of water, as may be gathered from Caspary's records given in the above cited papers on the opening and closing of clefts, as well as from direct measurement of circumferences.<sup>3</sup>

According to the figures in text-books of physics changes in the lengthwise dimension of wood due to a change of temperature are only slight as compared to changes resulting in transverse direction. The transverse contraction of wood is given as nearly the same as the linear contraction of ice. It has been suggested that different types of tree tissues contract at different rates and that the branches of trees are caused to move up and down by changes of temperature owing to a differential contraction and expansion of the tissues on the two sides.

The literature of branch movements of trees is rather meager and not generally known, as may be gathered from an article which appeared in 1904, entitled, "An Undescribed Thermometric Movement of the Branches in Shrubs and Trees,"<sup>4</sup> as well as from some recent correspondence with C. C. Trowbridge who has made a study of the subject but had found only Ganong's paper. The earliest published observations and experiments found on branch movements induced by changes in temperature were by Geleznov.<sup>5</sup> He noted that branches of certain trees sink during cold weather and rise again as it becomes warmer.

<sup>3</sup> "Crown-rot of Fruit Trees: Field Studies," N. Y. State Agri. Expt. Sta. Technical Bull., 23: 35-39, 1912.

<sup>4</sup> W. F. Ganong, *Ann. Bot.*, 18: 631-44, 1904.

<sup>5</sup> N. Geleznov, "Recherches sur la quantité et la répartition de l'eau dans la tige des plantes ligneuses," *Mélanges Biol. Acad. Imper. Sc. St. Petersb.*, 9: 667-85, 1877.

During a thaw branches of linden, birch, elm, and other epinastic species were cut and fixed in horizontal position by their bases, some with their lower sides uppermost; and the position of the tips was marked. As the temperature became lower the inverted branches moved in a direction opposite to that of the branches in normal position, indicating that the direction of movement depends on the make-up of the branches. It was noted, however, that although pine branches are hyponastic and linden branches epinastic, both bend downward as the temperature sinks, showing that the nature of the eccentricity could not be the cause of these movements.

The relative amounts of water contained in the wood of the lower and upper sides of branches gave no convincing results, although it seemed possible that this might have a causal relation to the movement. It was found that the wood on the upper side of pine branches had a greater water content than that on the lower, while in the case of birch and a number of other trees the wood on the underside contained more water than that on the upper. The water determinations were made once each month throughout the year and are interesting aside from any bearing they may have on branch movements. For instance, the bark on the larch was found to contain more water throughout the year than the wood; the wood often contains less water toward the distal end of branches, while the bark usually contains more.

Caspary also made some very interesting observations the year following the studies by Geleznov,<sup>6</sup> although the work was not published until much later. The positions of the ends of convenient branches of ten species of trees were marked on upright stakes driven in the ground and their locations redetermined about sun-up each day from November 29, 1865, to March 24, 1866. Heavy dew and rain were found to cause a slight depression of branches and snow induced considerable sink-

<sup>6</sup> R. Caspary, "Über die Veränderungen der Richtung der Äste hölziger Gewächse bewirkt durch niedrige Wärmegrade," *Internat. Hort. Exhibit Bot. Congress, London*, 3: 98-117, 1886.

ing. It was also noted that after a period of rather strong wind the branches drooped much more than was the case in a calm period having the same temperature. But even such influences failed to prevent the rise of branches on the occurrence of low temperature in case of species which normally raised their branches on the coming of cold weather. It was also found that branches were diverted to the right or left on some trees in proportion to the degree of cold. The branches of linden and those of conifers sank with the temperature, while those of *Pterocarya* and *Acer* rose as the temperature became lower. The branches of *Æsculus*, *Carpinus*, *Rhamnus* and *Pavia* rose on slight lowering of the temperature and sank when it became colder. The distal ends of the branches on nearly all of the trees under observation stood higher in spring than they did in the preceding fall. The eccentricity of the wood of branches was thought to have no relation to this movement, but it seemed that it might be due to a differential contraction and expansion of the upper and under sides of branches, and it was held that this difference in contraction must be distributed over the entire length rather than being confined to the crotch regions.

Ganong's<sup>7</sup> observations were more limited. He found that branches move or bend upward or toward the axis as the temperature sinks. He reports that the branches had a greater water content during warmer days of winter than during the colder ones and therefore the thermometric movement. According to the determinations by Geleznov the water content of the wood of *Pinus silvestris* reached a minimum in June and a maximum in October, while bark has its maximum in October and its minimum in April. *Acer platanoides* had a maximum water content in the wood in June and a minimum in October; that is, it was found that the minimum water in the wood does not occur in winter, but since his determinations were made monthly they throw no light on the validity of Ganong's inference that the movements depend on periodic variations in the water content. The most recent

contribution to this subject is by C. C. Trowbridge.<sup>8</sup> Although only a summary has appeared as yet it promises to be of interest not only because of its content, but also on account of the fact that it is from the physicist's standpoint. Owing to its brevity this summary as given in the proceedings of the Torrey Botanical Club is quoted here in full:

(1) That branch movements occur in certain trees, due to temperature changes below the freezing point of water, and that in certain other trees no movement whatever has been observed. (2) That the movements amount to as much as 3 or 4 ft. differences in the distance from the ground to the ends of certain curved branches which are in length of the order of 20 ft., these changes occurring through a range of 30 degrees below freezing. (3) That little, if any, movement takes place above freezing point of water, and that the movements begin soon after the temperature remains at this point for several hours. (4) That there is a considerable lag in the movement of the branches behind the temperature changes, although a difference in the rate of change of temperature is followed at once by a difference in the rate of change of the position of the branches. (5) That the movements are practically of equal magnitude in December, January and February, that is, the seasonal change is not a ruling factor in this movement.

According to Geleznov, then, tree branches may move either up or down as the temperature sinks. He found that eccentricity of the wood is not correlated with this movement, but that a difference in the water content of the wood on the upper and under sides of branches seems to be, yet he did not consider that an explanation of the movements but only a suggestive parallel. Caspary found three classes of trees in regard to the manner of branch movements: In one class the branches sink and in another they rise on lowering of the temperature and in the third class the branches rise as the temperature is lowered slightly but sink when it gets still colder. According to him the movements of branches result from a differential contraction of the

<sup>8</sup> "Branch Movements of Certain Trees in Freezing Temperatures," *Torrey*, 13: 86-87, 1913.

<sup>7</sup> *Loc. cit.*

under and upper sides of branches. These two investigators agree as to the main groups of trees in respect to the effect changes of temperature have on the position of their branches. It seems, therefore, that Ganong happened to use trees and shrubs which belonged to only one of these classes. The explanation advanced by Caspary is suggestive because it is based on a differential longitudinal contraction of the wood in branches. Some of his earlier studies<sup>9</sup> have shown that tree trunks undergo transverse contraction in proportion to the degree of cold and that the assumptions to the contrary are incorrect. That longitudinal contraction of wood takes place as the temperature is lowered is upheld by many general observations. Trees are frequently cleft in forks of the trunk during winter and these clefts open when it gets cold and close as warmer weather comes. In another connection the writer found that

crotch clefts were always at right angles to the branching and usually widest above, appearing as though the crotches had been split by driving in a thin wedge from above. In two instances where measurements were taken the component parts of the crotches had separated about 2 cm., which seems to indicate that there had also been a longitudinal contraction of the outer portions of the trunks, thus resulting in an outward bending of the branches.<sup>10</sup>

Caspary's observations on the lateral displacement of some tree branches also fit into his contraction theory, although he failed to note it, provided it is assumed that the trees on which this movement occurred had trunks with the so-called twisted grain, for in such a case longitudinal contraction would necessarily result in lateral movement of the attached branches.

In this connection it seems of interest to notice some of the peculiarities of arrangement of the tissues about the bases of branches that were studied by Jost.<sup>11</sup> He found that the cambium at the basal angles of branches

is not eliminated as the stems and branches grow in diameter, but that its cells and those of the tissues differentiating from the cambium glide between each other and also become shorter. In case of the adaxile side crowding and compression are more marked than on the abaxile side, apparently because the angle is usually much smaller. Sometimes the bark in the adaxile angle is not forced outward, but is included, and under such conditions the pressure in the angle compels the cambium under the included bark to cease growth. Most commonly, however, the wood-growth in the angle forces the bark outward and thereby induces a more rapid reduction in the cambial area and a greater increase in thickness per annual ring than on the abaxile side. In addition to gliding between each other, the cells in the adaxile side are turned at a tangential angle so that large groups of them come to lie almost horizontal or at right angles to the axis, while groups of cells from the branch and from the stem sides are forced in among these transverse cells of the crotch. Usually, then, no cambial cells are eliminated in branch-angles, but they are forced between their neighbors and complicated tangles result in which often large groups of cells come to lie in a more or less transverse direction. The ends of medullary rays vertical to each other in the base of branches come closer together and may even cross each other.

In view of the fact that the groups of partially transverse tissues at the base of a branch are probably under more or less pressure and because changes of temperature have a much greater effect upon transverse than upon longitudinal dimensions it seems possible that the differential contraction which according to Caspary is the cause of the thermometric branch-movements may be chiefly confined to the bases of branches and depend upon these peculiar gnarled growths described by Jost, and perhaps their arrangement about the base of a branch which is usually characteristic for a species, may determine whether a branch shall move up or down as the temperature sinks. The relative amounts of "spring" and "summer" wood in the under and upper sides

<sup>9</sup> *Loc. cit.*

<sup>10</sup> *Loc. cit.*, pp. 36-37.

<sup>11</sup> L. Jost, "Ueber einige Eigenthümlichkeiten des Cambiums der Bäume," *Bot. Zeit.*, 59: 1-24, 1901.

of annual rings at the bases of branches may also have a possible relation to the movements. At any rate, it seems more promising to seek for some anatomical differences between the upper and under sides of branches as the cause of the movement than to study their water content.

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### SPECIAL ARTICLES

#### "YELLOW" AND "AGOUTI" FACTORS IN MICE

SOME time ago Mr. A. H. Sturtevant<sup>1</sup> suggested the hypothesis that there is negative coupling between the "yellow" and the "agouti" factors in mice. At that time<sup>2</sup> I offered certain facts which appeared to me to give evidence contradictory to the hypothesis which he advanced.

I included in this evidence the data offered by certain matings of mice made by Miss F. M. Durham.<sup>3</sup> It now appears that I misunderstood the true meaning of her tables, which were somewhat ambiguous, and that accordingly the only remaining evidence which I possessed against Mr. Sturtevant's hypothesis was afforded by the results of certain matings which I made about five years ago.

It seemed, therefore, advisable to make crosses calculated to test his hypothesis with the stock which I have at present on hand.

The first of these matings was between wild agouti mice and yellow mice which did not carry the agouti factor. To use Sturtevant's terminology these individuals were as follows:

Yellows— $Yt\ yt$ ,  
Agouti— $yT\ yT$ .

Two sorts of individuals, yellow and agouti, are expected in equal numbers from such matings. The actual results were 14 yellow, 28 agouti. The yellows should on Sturtevant's hypothesis be of the formula  $Yt\ yT$  and form only two

sorts of gametes  $Yt$  and  $yT$ . Such yellows should by any non-yellow animal, or when mated *inter se*, give only two sorts of young, yellow and agouti. Actually they produced 23 yellow and 18 agouti young.

Thinking that possibly the *black* factor might be necessary to obtain such a result, I mated three homozygous dilute brown agouti animals with a single brown-eyed yellow (carrying no agouti). All these animals lack the factor for black. The first generation gave 11 yellows and 5 brown-agoutis. The yellows were then crossed with dilute *brown* animals which did not possess the factor for agouti. If according to Sturtevant's hypothesis there was negative coupling or repulsion between the yellow and agouti factors there would be only yellow and agouti young from such a mating. If, on the other hand, these factors were entirely independent we should have non-agouti young as well. The results follow.

	Yellow	Dilute Yellow	Brown Agouti	Dilute Brown Agouti	Brown	Dilute Brown
Observed.....	31	34	24	27	0	0
Expected by Sturtevant's hypothesis.	29	29	29	29	0	0
Expected by independent recombination.....	28.5	28.5	14.2	14.2	14.2	14.2

The conclusion is obvious that the factors for yellow and agouti are unable to go into the same gamete. On the other hand, the factors for "density" and "dilution" of pigmentation show no such relation to any other factors.

Since I have no reason to doubt the authenticity of the contradictory cases, in my own work, to which I have already referred, it seems probable that the factors for "yellow" and "agouti" are not absolutely incompatible, but that they may in rare cases occur in the same gamete. As a general thing, however, it seems that Sturtevant's hypothesis is correct and that a negative association exists between these two factors.

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<sup>1</sup> Sturtevant, A. H. (1912), *Am. Nat.*, Vol. 46, pp. 368-371.

<sup>2</sup> Little, C. C. (1912), *Am. Nat.*, Vol. 46, pp. 491-493.

<sup>3</sup> Durham, F. M. (1911), *Journal of Genetics*, Vol. 1, pp. 159-178.